

Remains of Land Birds from Lisianski Island, with Observations on the Terrestrial Avifauna of the Northwestern Hawaiian Islands¹

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ABSTRACT: Early nineteenth-century accounts suggest that there were ducks and rails on Lisianski Island, although neither were present in 1891 when the first ornithological collector visited the island. Excavations and surface searches on the island in 1990 uncovered numerous bones of the Laysan Duck (*Anas laysanensis* Rothschild), indicating that there once was a resident population. A single coracoid of a small rail (*Porzana*) probably came from one of the 45 individuals of Laysan Rail (*P. palmeri* Frohawk) that were introduced in 1913 and quickly died out, because no further evidence of rails or other land birds was found. Extinction of the duck may have been due to predation by survivors of mid-nineteenth-century shipwrecks and possibly to competition for food from introduced House Mice (*Mus musculus* Linnaeus). The land birds of the Northwestern Hawaiian Islands were derived partly from Asia and partly from species that were formerly widespread in the lowlands of the main Hawaiian Islands. They are not, therefore, a collection of ancient relicts of a montane biota as has been hypothesized. The terrestrial avifauna of Nihoa is depauperate even for an island of its size and may have suffered prehistoric human-caused extinctions.

THE NORTHWESTERN HAWAIIAN chain (Figure 1) comprises a far-flung group of small, mostly low islands that collectively present a hostile, or at best marginal, environment for most terrestrial organisms. Resident populations of land birds have been known with certainty only from the islands of Nihoa and Laysan. Even in this remote chain, prehistoric human interference with the biota may have been a factor, just as in the main Hawaiian Islands (Olson and James 1982, 1991, James and Olson 1991) and the rest of the Pacific (Milberg and Tyrberg 1993), because at least Nihoa and Necker are known to have been discovered and abandoned by Polynesians (Emory 1928, Clapp and Kridler 1977, Clapp et al. 1977, Cleghorn 1988). Reports of ducks and a possible rail on Lisianski in the first half of the nineteenth

century were never confirmed subsequently either by specimens or by sightings by scientifically reliable observers. Here we review these early accounts and supplement them with new data from investigations conducted on the island in 1990 by A.C.Z.

EARLY HISTORY OF LAND BIRDS ON LISIANSKI

Some notable biological events or observations in the history of Lisianski are summarized in Table 1. The first scientific visit to the island was that of the Russian ship *Moller*, commanded by Captain Stanikowitch, which passed through the Northwestern chain in 1828 and made landings at Gardner Pinnacles, Laysan (which the expedition named "Moller"), and Lisianski (on 3 April). There was no naturalist on board, but observations on bird life were made by the ship's surgeon, C. Isenbeck, and these were passed on to the ornithologist F. H. von Kittlitz, then sailing on the *Senjavin*, when the two met later in Kamchatka. Kittlitz (1834) published these notes, which were

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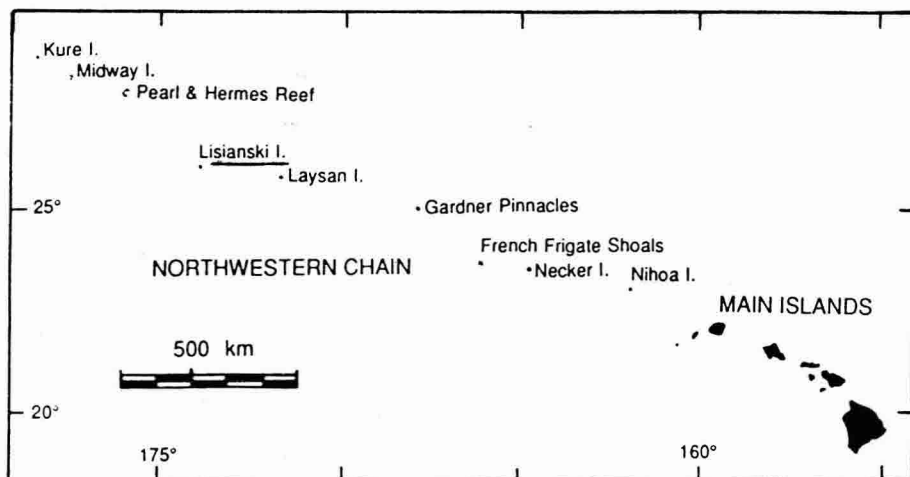


FIGURE 1. Map of the Hawaiian archipelago showing the position of Lisianski and other islands of the Northwestern Hawaiian chain (from Olson and James 1991).

TABLE 1

SOME IMPORTANT DATES IN THE BIOLOGICAL HISTORY OF LISIANSKI ISLAND, BASED LARGELY ON CLAPP AND WIRTZ (1975)

| YEAR | DATE | EVENT |
|--------------|-------------------|---|
| 1805 | 15 October | Discovery by the <i>Neva</i> , Captain Urey Lisianski |
| 1828 | 3 April | Visit by the <i>Moller</i> , observations of birds by C. Isenbeck |
| 1844 | 12 April | Wreck of <i>Holder Borden</i> , predation on ducks, probable introduction of House Mice |
| 1846 | 24 May | Wreck of <i>Konohasset</i> , many "mice" reported present, no mention of ducks |
| 1891 | 29 June–7 July | Birds collected for Rothschild by Henry Palmer; no ducks or rails present, no mention of mice |
| 1893 | Summer | John Cameron noted "myriads of mice" |
| [?1904–1909] | | Rabbits presumably introduced in this period (a few definitely present by January 1910) |
| 1904 | 8 January–16 June | Japanese plumage hunters kill many seabirds |
| 1909–1910 | April?–19 January | Japanese plumage hunters again kill many seabirds |
| 1913 | 12 March | Visit by <i>Thetis</i> , observations on birds, 45 Laysan Rails introduced, rabbits abundant |
| 1914 | 12 September | Visit by <i>Thetis</i> , vegetation essentially eliminated by rabbits, which were dying of starvation |
| 1915 | 24 March | Visit by <i>Thetis</i> , last seven rabbits removed, Laysan Rails still present |
| 1916 | 5 February | Visit by <i>Thetis</i> , one or two Laysan Rails seen |
| 1923 | 15–20 May | <i>Tanager</i> expedition, Laysan Rails and mice absent |

later extracted in part and translated into English by Rothschild (1893).

Isenbeck made creditable observations of various seabirds and shorebirds and remarked on five species of land birds on Laysan, though at least in one instance his description

cannot easily be reconciled with the actual appearance of the bird in question (the quotes below are from Rothschild 1893:v–vi). His "small Sparrow-like bird, brownish grey above, yellowish green below" and the "small red bird with black wings" are clearly

the Laysan Finch (*Telespiza cantans* Wilson) and the Laysan Apapane (*Himatione freethii* Rothschild). He also mentioned "A small bird, somewhat resembling a Humming-bird; like it hovering in the air. Brownish, glossy greenish from beneath." Rothschild dismissed this as nonexistent, but if one discounts the glossy green underparts the description could possibly apply to the Laysan Millerbird (*Acrocephalus familiaris* Rothschild). Isenbeck was careful to note that these three species did *not* occur on Lisianski.

On the other hand, he mentioned "A species of Duck, with no conspicuous plumage, living in small flocks on Moller [= Laysan] and Lisiansky, but not breeding." And then "A kind of Fowl, about as large as a Ptarmigan; mixed grey and brown; running on the ground, singly, but at the same time rather numerous, on Moller and Lisianski; very rapid and rather shy. Eggs were not found." The first description, at least as it applies to the bird of Laysan, is clearly the Laysan Duck (*Anas laysanensis* Rothschild). The fowl-like bird Rothschild thought could only be the Laysan Rail (*Porzana palmeri* Frohawk), although Clapp and Wirtz (1975:115) considered that "the description might also fit the Bristle-thighed Curlew [*Numenius tahitiensis* Gmelin]." This last supposition we reject, because the description does not fit a curlew and because Isenbeck mentioned a "species of snipe" and "a species of sandpiper" and surely would not have referred to a curlew as a "fowl." The reference to the bird's being the size of a ptarmigan ("*Schneehuhn*" in Kittlitz 1834:124 [= *Lagopus* spp.]) must be a result of faulty recollection or faulty communication between Isenbeck and Kittlitz, because the former can hardly have overlooked the rail on Laysan. The presence of a duck and the presumed rail on Lisianski was reaffirmed in Kittlitz's list of the birds of Laysan (Kittlitz 1834:125–126), in which it is stated that all of the species also occurred on Lisianski except the three that are equivalent to the finch, apapane, and millerbird.

Although there was never again any report of a rail from Lisianski, survivors of the wreck of the *Holder Borden*, who were

stranded on Lisianski in 1844, found "wild ducks," which apparently they ate, to be "plentiful" and "peculiarly inclined to renounce their wild and roving propensities and adopt the domestic habits of civilized life. A flock of 40 had attached themselves to the settlement" (quotations from Clapp and Wirtz 1975:113). It was also at that time that House Mice (*Mus musculus* Linnaeus) are thought to have been introduced to the island. No subsequent visitors ever mentioned ducks on Lisianski, and they may have been exterminated either by the *Holder Borden* survivors or by those from the wreck of the *Konohasset* 2 yr later.

Some authors have accepted that there was a population of *Anas laysanensis* on Lisianski (e.g., Warner 1963), but other sources make no mention even of the possibility (American Ornithologists' Union 1983).

EXCAVATIONS ON LISIANSKI

Lisianski Island (Figure 2) is a small (1.8 km²) emergent portion of an extensive coral-line-algal reef atoll surmounting a now-submerged eroded volcano that formed about 20 million yr ago. The beaches of reef-sand that encircle the island are backed by a vegetated sand berm 2–3 m high. From the berm inland, especially at the northern and southern ends of the island, broad arcs of vegetated or bare, loose sand rise 7–12 m above current sea level. The entire center of the island is depressed, with the lowest southern region lying only a little more than a meter above sea level.

A.C.Z. carried out archeological and paleontological investigations on Lisianski between 10 June and 11 August 1990 (Ziegler, unpubl. data: 1990a, Search for evidence of early Hawaiian presence on Lisianski Island, Northwestern Hawaiian Islands, summer 1990, report prepared for State of Hawaii Office of Hawaiian Affairs; 1990b, Biological observations on Lisianski Island, Hawaiian Islands National Refuge, summer 1990, report prepared for U.S. Fish and Wildlife Service, Pacific Islands Office). Subsurface

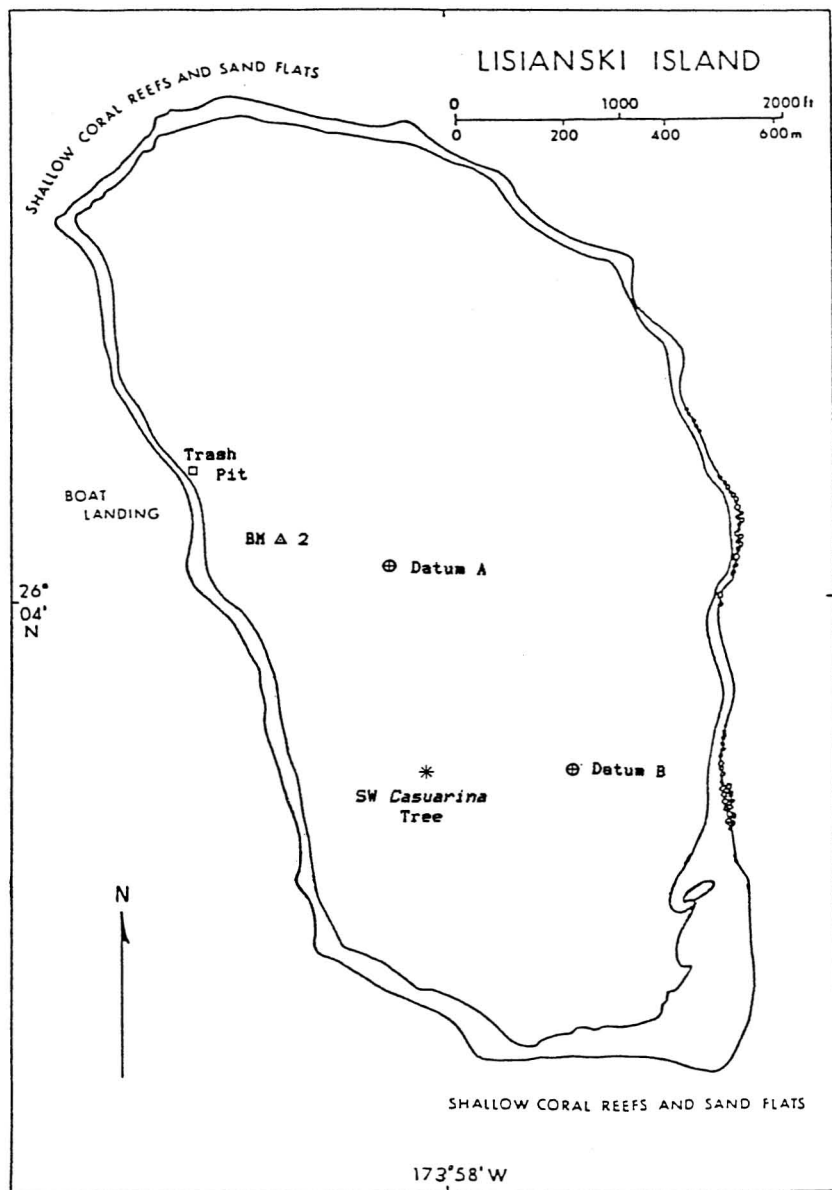


FIGURE 2. Map of Lisianski Island showing the location of excavation sites (from Ziegler, unpubl. data: 1990a).

excavations were made in three widely separated locations (Figure 2). The "Trash Pit" was a stratigraphically uncontrolled exploratory excavation of the beach berm carried out in conjunction with setting up camp nearby. That excavation, about 1 m in diameter, extended from a surface elevation of ca. 3 m, down through ca. 1.5 m of loose sand.

Excavated matrix was field-sieved through stacked wire screens of 6-mm and 3-mm mesh, but all of the relatively few bones recovered were of common indigenous oceanic birds and inshore fishes. Most of the fish bones probably originated as food of seabirds or Hawaiian Monk Seals (*Monachus schauinslandi* Matschie) that frequent beach areas of

Lisianski. Many of the fish bones and teeth show the digestive corrosion characteristic of remains recovered from scat or regurgitated stomach contents of seals on several Northwestern Hawaiian islands (A.C.Z. pers. obs.). That excavation has no further relevance to this report.

An inland excavation, Datum A, was established 200 m east and 50 m south of U.S. Coast and Geodetic Survey (USCGS) Bench Mark 2, to test a relatively high portion of the depressed center of the island. The datum elevation, as measured with a mason's spirit level, cord, and stakes from the bench mark height of 6.38 m above sea level (ASL), was ca. 4.9 m. A single standard meter-square excavation unit (designated as Pit S0/W1 in Table 2) was dug to a depth of 210 cm below datum.

A third excavation, Datum B (elevation ca. 1.1 m ASL), was dug in a lower inland area to the south. Its position could not be established except in relation to a small group of dead introduced common ironwood (*Casuarina equisetifolia* Linnaeus) trees in the southwestern quadrant of the island (265 m east and 5 m north of the easternmost of those trees [a USCGS Triangulation Station supposed to have been established in that area in 1931 could not be found]). A total of 8 square meters in the immediate vicinity of this datum was excavated to various stratigraphic levels, as were portions of nine similar-sized units located several meters to the southwest and an additional pit located 50 m north and 70 m east of the datum.

The surface layer at both Datum A and Datum B consisted of disturbed, loose, grayish buff, calcareous sand of varying thickness (maximum of 130 cm at Datum A and ca. 40–60 cm at Datum B). At Datum A this loose sand rested on a variably cemented layer of brownish sand and water-smoothed, coralline-algal reef cobbles. This layer overlaid a deposit of clean yellowish sand containing water-worn shells of marine mollusks and reef cobbles but lacking vertebrate remains. This lowest layer apparently represents the floor of an open ocean "inlet" (see Guinther 1974:320 for definitions) that formerly occupied at least part of the low interior of the island during a time of higher

sea level. It appears likely that Lisianski never possessed an often-hypothesized inland "pond" similar to the present hypersaline one of Laysan (Ziegler, unpubl. data: 1990b:26).

The same three layers occurred at Datum B, but with a fourth component interposed. On the surface of the cemented sand-and-cobble layer, which here was uniformly very strongly indurated and dark brown, was a thin layer of somewhat compacted, very dark brown soil that did not reach the tops of many of the larger underlying cobbles. It reached a maximum thickness of ca. 10 cm, although averaging only about 3–4 cm. This soil, judging from its unusually dark coloration and apparent ability to retain moisture, is highly humic; presumably it was formed from decayed hydrophilic vegetation once growing in that area, which closely overlies the island's freshwater lens that was formerly tapped for drinking water by nineteenth-century shipwreck survivors.

Only the pit at Datum A and two at Datum B (S2/W4 and N50/E70) were extended through the cemented sand-and-cobble layer to reveal the full stratigraphic range. All matrix from each arbitrary 10-cm or 20-cm level or natural stratum was sieved through 6-mm and 3-mm mesh. Of the other 16 excavation units at Datum B, seven were dug only through the dark soil layer, which was always screened, although the overlying loose sand of only two units was similarly processed. The remaining nine units had only the loose sand removed, leaving the surface of the dark soil layer exposed but intact. All of the loose sand not screened was at least scanned during excavation, and all observed bones and other material of special interest were removed.

Five duck bones (Table 2) were recovered at Datum A: four from the disturbed loose sand and one from the underlying variably indurated layer. No human cultural evidence that would serve to date these remains was found at that site. A very few fragments of charcoal, apparently from nodes of an abundant local grass, and a short branch segment of shrub that was scattered in the disturbed loose sand probably resulted from a brush fire, which may or may not have been human-related. A single burned scapula of a

TABLE 2
EXCAVATION DATA FOR BONES OF LAND BIRDS RECOVERED ON LISIANSKI BY ZIEGLER IN 1990

| SPECIES | BPBM | ELEMENT | DATUM | PIT | DEPTH (cm below datum) | SEDIMENT | LENGTH (mm) |
|-------------------------|--------|------------------|-------|-------|---------------------------|-------------------------|----------------|
| <i>Anas</i> | | | | | | | |
| <i>laysanensis</i> | | | | | | | |
| | 178522 | R pterygoid | A | S0/W1 | 110–130 | Loose sand | |
| | 178523 | L quadrate frag. | A | S0/W1 | 70–90 | Loose sand | |
| | 178524 | L mandible frag. | B | S1/W3 | 40–60 | Dark soil | |
| | 178525 | R scapula frag. | A | S0/W1 | 130–150 | Brown indurated sand | |
| | 178526 | R coracoid | A | S0/W1 | 110–130 | Loose sand | 34.0 |
| | 178527 | R coracoid frag. | | Mound | Surface | Loose sand | |
| | 178528 | L coracoid | | Mound | Surface | Loose sand | 34.7 |
| | 178529 | L humerus | | Berm | Surface | Loose sand | 69.3 |
| | 178530 | Rd humerus | B | S1/W2 | 40–60 | Dark soil | |
| | 178531 | Ld ulna | B | S2/W4 | 50–60 | Dark soil | |
| | 178532 | Ld ulna | B | S0/W3 | 45–60 | Dark soil | |
| | 178533 | Rp radius | B | S2/W4 | 50–60 | Loose sand | |
| | 178534 | Lp radius | B | S2/W3 | 40–70 | Dark soil | |
| | 178535 | Ld radius | B | S1/W3 | 40–60 | Dark soil | |
| | 178536 | Lp CMC | A | S0/W1 | 90–110 | Loose sand | |
| | 178537 | Rd CMC | B | S2/W3 | 40–70 | Dark soil | |
| | 178538 | Ld CMC | B | S1/W2 | 40–60 | Dark soil | |
| | 178539 | L CMC | B | S0/W2 | 40–60 | Dark soil | 33.5 |
| | 178540 | L CMC | | Mound | Surface | Loose sand | 34.3 |
| | 178541 | L femur | | Mound | Surface | Loose sand | 40.0 |
| | 178542 | R femur | | Mound | Surface | Loose sand | 42.5 |
| | 178543 | Lp femur | | Mound | Surface | Loose sand | |
| | 178544 | L femur | | Mound | Surface | Loose sand | 40.2 |
| | 178545 | R femur | | Mound | Surface | Loose sand | 41.6 |
| | 178546 | L femur | | Mound | Surface | Loose sand | 37.4 |
| | 178547 | R femur | | Mound | Surface | Loose sand | 39.9 |
| | 178548 | Ld femur | B | S2/W3 | 40–70 | Dark soil | |
| | 178549 | L femur | B | S1/W3 | 40–60 | Dark soil | 41.8 |
| | 178550 | Rp tibia | | Mound | Surface | Loose sand | |
| | 178551 | Lp tibia | | Mound | Surface | Loose sand | |
| | 178552 | L TMT | | Mound | Surface | Loose sand | 33.6 |
| | 178553 | L TMT | | Mound | Surface | Loose sand | 34.4 |
| | 178554 | L TMT | | Mound | Surface | Loose sand | 33.7 |
| | 178555 | Rd TMT | B | S2/W2 | 50–65 | Dark soil | |
| | 178556 | Rp TMT | B | S2/W2 | 50–65 | Dark soil | |
| | 178557 | Ld TMT | B | S0/W3 | 45–60 | Dark soil | |
| | 178558 | Lp TMT | B | S0/W3 | 45–60 | Dark soil | |
| | 178559 | R coracoid | B | S2/W4 | 56 | Cemented sand /soil | 39.6 |
| | 178560 | Ls humerus | B | S1/W3 | 0–55 | Loose sand | |
| <i>?Porzana palmeri</i> | | | | | | | |
| | 178562 | L coracoid | B | S2/W4 | 30–40 | Loose sand | 11.3 |

NOTE: Length measurements are given for complete specimens. Abbreviations: CMC, carpometacarpus; TMT, tarsometatarsus; L, left; R, right; p, proximal; d, distal; s, shaft; frag., fragment.

Bonin Petrel (*Pterodroma hypoleuca* Salvin) could have been carried to the area from a relatively enormous concentration of historically burned bird bones in the vicinity of Pit

N50/E70 of Datum B by a Brown Noddy (*Anous stolidus* Linnaeus), a species that was noted occasionally to transport smaller bird bones to its nesting sites on the ground.

In the Datum B area, abundant evidence of human occupation was highly informative regarding the relative age of land bird remains. The dark soil layer seems to represent the uppermost stratigraphic layer present when humans first arrived on the island. Numerous scales and bones of fish, as well as relatively abundant small pieces of charcoal from plants larger than grasses and small shrubs, are widespread over the soil's surface; although these are sometimes partially pressed into the top of the thin soil layer, they do not occur entirely within it. Also, all other culturally related items—most of them obviously

historic in age and dating largely from the 1909–1910 period of Japanese plumage-hunter occupation (Ziegler, unpubl. data: 1990a)—were situated either on, or stratigraphically above, this dark soil layer. If tangible evidence of Polynesian habitation exists on the island, the examination of a greater expanse of the surface of this soil layer seems the method most likely to reveal it, primarily because of the proximity of potable water that would have been requisite for an extended prehistoric visit. The position of the historic artifactual material indicates that the layer of loose sand overlying the

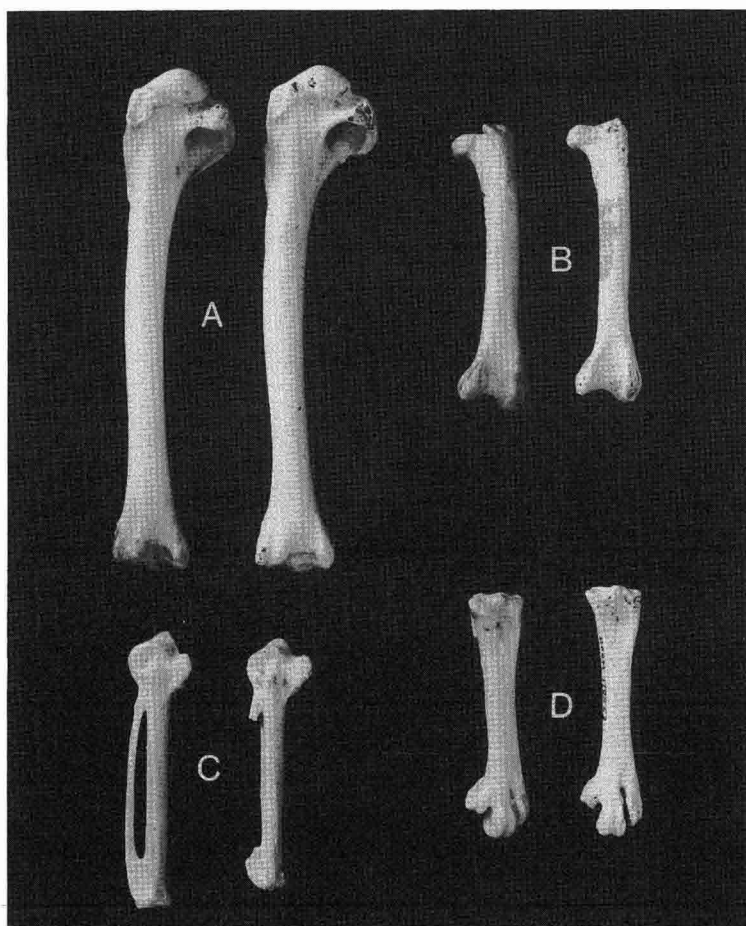


FIGURE 3. Bones of Laysan Duck (*Anas laysanensis*) from Lisianski Island (on the right in each pair) compared with a modern skeletal specimen (USNM 611802): A, humeri (BPBM 178529); B, femora (BPBM 178541); C, carpometacarpal (BPBM 178540); D, tarsometatarsi (BPBM 178553). Natural size.

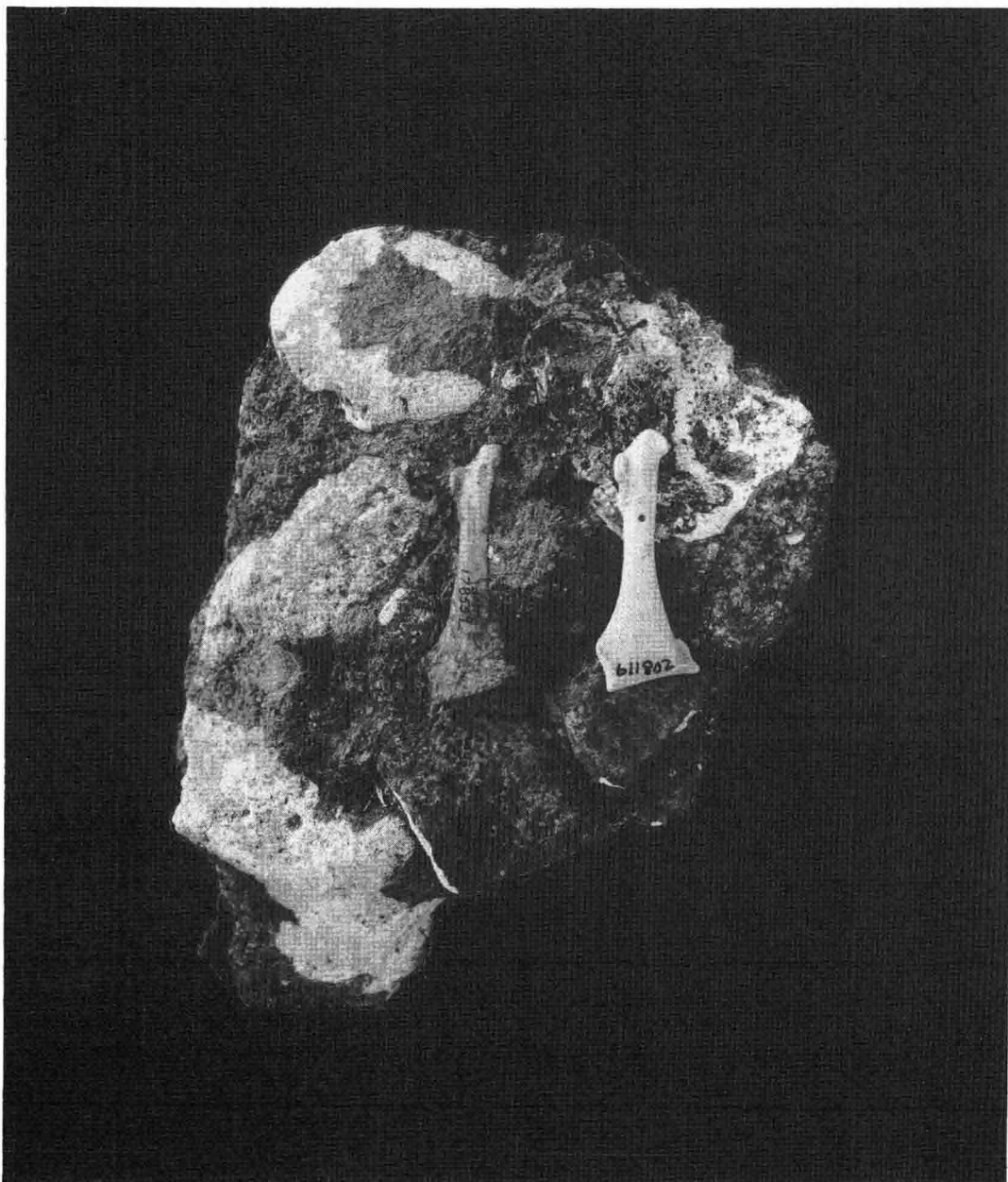


FIGURE 4. Coracoid of Laysan Duck (*Anas laysanensis*) from Lisianski Island (on the left [BFBM 176559]), still embedded in a conglomerate of coral rubble and indurated sandy/peaty sediment, compared with a modern skeletal specimen (USNM 611802). Natural size.

dark soil, at least in the vicinity of Datum B, accumulated since the Japanese plumage hunters' departure in early 1910 and is undoubtedly sand that blew into this low area

from higher levels denuded of vegetation by introduced European Rabbits (*Oryctolagus cuniculus* Linnaeus).

The Datum B excavations yielded 18 of the

39 duck bones (Table 2): two from the overlying disturbed loose sand, 15 from within the dark soil layer, and one incorporated into the strongly cemented sand-and-cobble layer beneath the soil (Figures 3, 4). This stratigraphic distribution thus appears unquestionably to document that there was a duck on Lisianski before human arrival.

On the other hand, the single rail bone (Figure 5) was found in the upper layer of disturbed loose sand; no rail remains were obtained from the dark soil or the layer beneath it. This strongly suggests that no rail existed before humans arrived on Lisianski. Before its extinction, the small flightless rail of Laysan was a relatively abundant animal. If a similar bird had naturally inhabited Lisianski, we would expect its bones to be well represented, especially in the dark soil layer. The possibility that the rail coracoid came from one of the 45 individuals of Laysan Rail imported to Lisianski in early 1913 (see later in this paper and Table 1) is strengthened by

the fact that it was recovered in the generally lowest and relatively wettest part of the island. This area probably was the last to retain some type of vegetation and insects during the period from 1914 to 1916 when populations of introduced rabbits, rails, and House Mice were declining to extinction, thus attracting and concentrating the starving or otherwise moribund animals.

Sixteen of the duck bones listed in Table 2 were found other than in excavations, which requires some explanation. All three species of petrels and shearwaters (Procellariidae) that breed on Lisianski dig nesting burrows each breeding season that may extend 2 m in length and 0.5 m below the surface. The sand thrown out during excavation of these burrows forms a bare mound, which in the case of the larger species can reach almost 1 m in diameter and 0.3 m in height. These low "shearwater mounds" of various ages essentially cover the interior of Lisianski, and many are kept clear of creeping vegetation for a number of months each year during their use as nesting sites and chick-feeding stations by the two breeding species of albatrosses (Diomedidae).

In the process of excavating burrows, the procellariids also move previously buried objects, such as smaller bones and mollusk shells, to the surface, where they are easily visible on the surface of unvegetated mounds. Most such material originates either in the continually disturbed loose sand layer or, in areas where it occurs, in the underlying dark soil layer. Virtually all of the 16 duck bones not assigned to a particular datum in Table 2 were picked up on the surface of shearwater mounds. A.C.Z. made many random searches of almost all areas of the island specifically for this purpose. The wide distribution of duck bones over the island in surface deposits suggests that most of them came from naturally dying birds rather than ones that served as human food. No bones of rail or other small land birds were found during this prospecting, nor would they necessarily have been overlooked, because the small bones of mice were easily noticed.

Thousands of unmodified bones of seabirds, as well as a much smaller number of bones of common migratory shorebirds

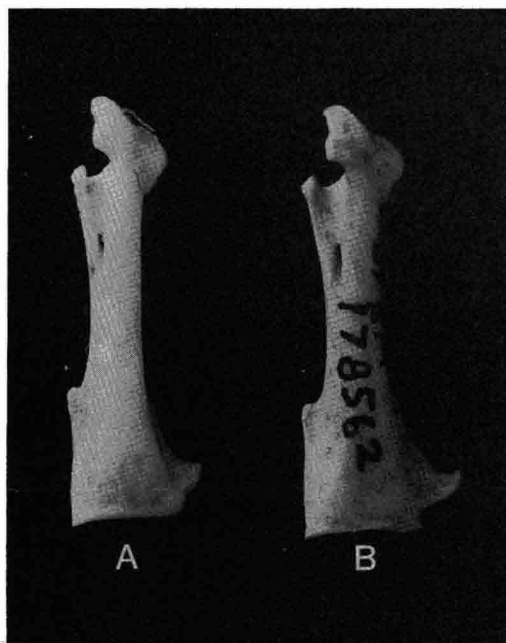


FIGURE 5. Coracoid of a Laysan Rail (A: *Porzana palmeri* [USNM 289241]) compared with a rail coracoid from Lisianski (B: BFBM 178562) that probably came from one of the Laysan Rails introduced to the island in 1913. 5 × natural size.

(Scolopacidae, Charadriidae) were recovered in all facets of the investigation. Insofar as their condition allowed, these were identified to species, although bones of albatrosses, boobies (Sulidae), and terns (Laridae) were determined only to family level. All nine of the taxa previously recorded by Clapp and Wirtz (1975:51–54) as breeding on, or commonly migrating to, Lisianski were recovered in the excavations, with the exception of the Red-tailed Tropicbird (*Phaethon rubricauda* Boddaert). Seven of these species were represented in the presumed prehuman-occupation stratigraphic levels. In addition, Tristram's Storm-petrel (*Oceanodroma tristrami* Salvin), previously unreported from Lisianski but known to nest on several other Northwestern Hawaiian Islands, was identified in both pre- and posthuman-occupation deposits. No other seabird or shorebird remains apart from species already recorded for the island were obtained.

THE LAND BIRD REMAINS

Laysan Duck (Anas laysanensis)

Figures 3, 4

MATERIAL EXAMINED. See Table 2.

DISCUSSION. The total number of duck bones recovered is 39. Considering the sample as a whole, there is a minimum of five individuals represented, although if differences in size, preservation, and excavation site are taken into account, the actual number of individuals represented is certainly much higher, in excess of 11.

In size and overall morphology, these bones are indistinguishable from those of the Laysan Duck, except that the carpometacarpus may be smaller than average for that species. All existing skeletons of *Anas laysanensis* postdate the extreme genetic bottleneck that the species passed through after the turn of the current century, when the population on Laysan was reduced to 14 or fewer individuals (Warner 1963). Thus, the available modern specimens may not be representative of the amount of skeletal variation that existed in the species before 1900.

At least one tarsometatarsus collected on Lisianski is from a juvenile, though probably volant, individual, which, in conjunction with the relative abundance of bones and the early reports, provides a strong indication that there was a resident population of *Anas laysanensis* on Lisianski in the nineteenth century.

?*Laysan Rail (Porzana palmeri)*

Figure 5

MATERIAL EXAMINED. Complete left coracoid, BPBM 178562.

DISCUSSION. Only a single bone of a rail was discovered in the excavations on Lisianski. This is similar in size (length, 11.3 mm; width of sternal articulation, 3.1) to the coracoid in the Laysan Rail ($n = 8$): length, 10.5–11.2 (mean 10.9); width of sternal articulation, 2.7–3.4 (mean 2.9). Although the Lisianski coracoid shows some differences in the shape and extent of the sterno-coracoidal process and in the position of the procoracoid foramen from the individual of *P. palmeri* with which it is compared in Figure 5, there is variation in these features in other individuals, so that the Lisianski specimen probably falls within the range of variation of *P. palmeri*.

This bone probably came from one of the 45 Laysan Rails that were introduced on Lisianski in March 1913. These apparently did not reproduce and by February 1916, when no vegetation was left on the island because of introduced rabbits, only one or two rails were seen (Clapp and Wirtz 1975:115 [the 1916 date, although mentioned in the text, is omitted from their appendices listing scientific visits and their results]). Although the chances of finding even a single bone of one of these few individuals would seem to be small, in certain parts of the island they would have been enhanced for reasons discussed previously. That this bone was found at all suggests that the sampling effort was probably sufficient to have revealed an indigenous rail had there actually been one.

Although Isenbeck's account in 1828 seems a rather positive assertion that a rail similar to the Laysan Rail was present on Lisianski,

the rather strong negative evidence now available suggests that we should perhaps attribute this to erroneous recollection or faulty communication between Isenbeck and Kittlitz.

EXTINCTION OF LAND BIRDS ON LISIANSKI

Bone remains abundantly confirm the former presence of the Laysan Duck on Lisianski, but apart from the single rail bone, no evidence of any other land birds was recovered, nor was any certain evidence found for previous inhabitation by Polynesians (Ziegler, unpubl. data: 1990a,b).

The duck was last reported in 1844, and the only mention of a putative rail was in 1828. It is certain that neither duck nor rail remained by 1891, when the island was visited by a thorough ornithological collector. It is conceivable that the ducks were simply hunted to extinction by the survivors of the two successive shipwrecks in 1844 and 1846. Apart from direct human predation, the only other factor that we are aware of that may have influenced extinction of land birds on Lisianski was the introduction of *Mus musculus*. Mice were reported on Lisianski in 1846 in the account of the wreck of the *Konohasset* (Clapp and Wirtz 1975). These were presumed to have come from the wreck of the *Holder Borden* 2 yr previously. The only other mention of mice is in the account of John Cameron, who visited the island in the summer of 1893 (Farrell 1928). This narrative is so vivid and droll that it bears repeating in full:

We had settled ourselves for an appetizing supper of fresh food when myriads of mice attacked our meal ravenously and utterly without fear. Drive them away we could not; we slaughtered them by hundreds, yet they would not be denied. A full hour elapsed before we could eat in some semblance of peace; then each of us had to hold his food in one hand and a stick in the other. During the night the pests continually galloped over us; they did not, however, bite us, though that seems re-

markable, since there was little on the island for them to eat, unless they devoured one another.

By day we were not molested. In preparation for the certain onslaught of the next evening we brought the ship's cat ashore. Surely he would protect us. Not so. As the gloaming fell the mice swarmed upon us in numbers exceeding those of the preceding night. Some mouse runner with a fiery cross must have dashed about the island to summon the clans. Our cat began to kill in a feline paradise: here were all the dreams of the cat family come true: mice in impossible numbers, mice of incredible boldness. In a whirlwind of activity Tom slaughtered, too engrossed to bother with torturing his tiny victims. Yet the armies thronged too rapidly for him. Over his face crept disgust, dismay, fear as of the supernatural. Soon he sat himself on his haunches and stared at us; surrounded by windrows of dead mice, he let the wee animals run unharmed between his paws. The beasties had conquered: we removed our camp to the beach and dug a moat, which soon filled with sea water, as a protection against them. Only one succeeded in crossing the ditch. It was pointed out to Tom, but he would not touch it. (Farrell 1928: 397–398)

Clapp and Wirtz (1975) did not consider either of the reports of mice on Lisianski to be reliable. The first they thought could have pertained to the Polynesian Rat, *Rattus exulans* Peale. Because neither Palmer nor Munro, who were on Lisianski 2 yr before Cameron, mentioned mice, nor did any of the expeditions that followed them, Clapp and Wirtz considered that Cameron had confounded the island on which the mouse incident occurred, because his recollections were put down after many years had passed. This overlooks the fact that except for Midway, to which *Mus musculus* was introduced at an undetermined date before 1941, mice are unknown on any of the other islands of the Northwestern chain (Amerson 1971,

Clapp 1972, Woodward 1972, Ely and Clapp 1973, Amerson et al. 1974, Clapp and Kridler 1977, Clapp et al. 1977, Tomich 1986). Furthermore, Cameron's experience seems to have been pretty well grounded in memory, because he epitomized two of the Northwestern islands as "Lisiansky of the Mice, Laysan of the Birds!" (Farrell 1928:399).

A.C.Z.'s investigations removed all doubt as to the former presence and identity of a rodent on Lisianski, because he found abundant remains of *Mus musculus*, but none of *Rattus* (Ziegler, unpubl. data: 1990a,b). What he reported as two or more skeletons (later determined as a minimum of eight individuals) found in a bottle dating from the latter period of Japanese feather poachers establishes that mice were still present in 1910 (Ziegler, unpubl. data: 1990a:43). Wetmore (1925:104) alluded to an earlier mention of some type of "rat" on Lisianski, doubtless having its basis in *Mus musculus*, but he reported that no rodent of any kind was seen during the 6-day visit of the *Tanager* expedition in 1923.

Although *Mus musculus* is not usually implicated in the extinction of insular land birds, as rats (*Rattus* spp.) frequently are (e.g., Atkinson 1977), in numbers such as described by Cameron they could have had a deleterious effect, if only in reducing the potential food supply for land birds. It is worth considering that neither mice nor rats colonized Laysan, where the native land birds survived all the other insults that humanity hurled at them until rabbits were introduced and denuded the island of vegetation, whereupon three species were exterminated (Ely and Clapp 1973). The same fate befell Lisianski (Clapp and Wirtz 1975), but by the time rabbits were released there, land birds had already vanished.

AN OVERVIEW OF THE LAND BIRDS OF THE NORTHWESTERN HAWAIIAN CHAIN

Apart from bats, the only terrestrial vertebrates to arrive unaided in any of the Hawaiian Islands are birds. Only three of the islands of the Northwestern chain are known

to have supported resident populations of land birds—Nihoa, Laysan, and now Lisianski. It is now well established that massive extinction of species of birds among the main Hawaiian Islands took place prehistorically in the period after Polynesian colonization (James and Olson 1991, Olson and James 1991). Although it is also known that prehistoric humans discovered and abandoned at least the two easternmost islands of the Northwestern chain—Nihoa and Necker (Cleghorn 1988)—it is not clear yet to what extent prehistoric human activities may have reduced the diversity of land birds there or elsewhere in the Northwestern chain. There is no archeological evidence of previous Polynesian occupation of any of the islands west of Necker. Laysan, which had five species of land birds in an area of only 3.97 km², may be presumed to have had an intact avifauna at historic discovery in the early nineteenth century and well into the twentieth century. Because of unsuitable conditions for human survival, Gardner Pinnacles and French Frigate Shoals are unlikely to have been settled by Polynesians even had they been discovered by them. Necker probably could not have supported land birds because of its small size (ca. 0.2 km²) and lack of soil and vegetation. Thus, Nihoa remains the only island of the Northwestern chain where prehistoric humans are likely to have had an impact on land birds.

Anas laysanensis has always been regarded as an endemic to Laysan. We have now shown that it also once resided on Lisianski. Furthermore, skeletons, including juveniles, have been recovered in lava tubes on Maui and Hawai'i that appear to be indistinguishable from those of the Laysan Duck (S.L.O. and H. F. James, unpubl. data), whereas the larger Hawaiian Duck (*Anas wyvilliana* Sclater), which may be of more recent origin, does not occur in those sites. The identity of these ducks should be considered hypothetical until proper morphological and biochemical studies of them have been undertaken, but it appears as if the Laysan Duck may have been widespread in the main archipelago and once lived even in forested situations at fairly high elevations, far from water. Because of such

adaptability, a population perhaps could have existed on Nihoa as well. That there was no apparent differentiation, at least osteologically, in the populations from Laysan and Lisianski, compared with those of the main islands, suggests that the Northwestern populations either were of recent origin or were supplemented fairly regularly by immigrants from the main islands.

The Laysan Rail was flightless and thus certainly an endemic at some level. It is probably a derivative of the Old World species *Porzana pusilla* Pallas (Olson 1973a,b) and most likely arrived at Laysan from the west. The same invading stock may also have given rise to some of the smaller flightless rails of the main Hawaiian Islands (Olson and James 1991). Because a rail could colonize and thrive on such a low, inhospitable islet as Laysan, a rail might also be predicted on Nihoa, which, although smaller (0.7 km²), is higher and has more diverse vegetation.

The Laysan and Nihoa Millerbirds (*Acrocephalus familiaris* and *A. kingi* Wetmore [usually considered conspecific subspecies]) are the only Hawaiian representatives of the Old World warbler family Sylviidae and, like the Laysan Rail, certainly arrived from the west. There is as yet no fossil evidence to indicate that any representative of the genus ever established itself in the main islands, nor any reason to expect that other populations existed elsewhere in the Northwestern chain.

The so-called Laysan and Nihoa finches (*Telespiza cantans* and *T. ultima* Bryan), although once considered subspecies of a single species, are quite distinct from each other (Banks and Laybourne 1977, Olson and James 1982, James and Olson 1991). Like the Laysan Duck, they traditionally were considered to be autochthonous endemics to their respective islands, but, also like the duck, have been found as fossils in the main islands, whence they must have emigrated relatively recently. Laysan Finches were released on Eastern and probably also Sand Island of Midway Atoll (total area 5.2 km²) in 1891 and 1905 and established a successful population there until the islands were overrun by rats in the 1940s (Berger 1981). The species also was introduced successfully to Pearl

and Hermes Reef (0.3 km²) in 1967, where it still survives (Conant 1988). The Nihoa Finch was introduced to French Frigate Shoals (0.2 km²) also in 1967 (Berger 1981), but declined to extinction by about the late 1970s (S. Conant, pers. comm.). These instances show that at least some islands in the Northwestern chain with no known historic populations of land birds are capable of supporting at least a single species over a period of a few decades.

The Laysan Apapane is usually considered to be an endemic subspecies of the Apapane (*H. sanguinea* Gmelin), which occurs virtually throughout the main islands with no geographic variation. The plumage differences of *H. freethii* are probably mostly caused by fading from the intense sunlight of Laysan, but preliminary examination of its cranial osteology indicates that it is distinct and possibly more primitive than *H. sanguinea* (H. F. James and S.L.O., unpubl. data). If so, then perhaps it is a relict of an earlier evolutionary stage, rather than being specialized for the particular conditions of Laysan. If an Apapane could survive on Laysan, there could have been a niche for this or some other nectarivorous bird on Nihoa as well.

With only two species of land birds (the finch and the millerbird), the avifauna of Nihoa seems depauperate compared with what might be expected. Human predation and perhaps habitat alteration might have caused the disappearance of a duck or a flightless rail. On the other hand, it is difficult to envision a mechanism of extinction of a small arboreal passerine such as an Apapane that would not have affected at least the millerbird as well. A careful paleontological survey of Nihoa is much to be desired.

Schlanger and Gillett (1976:205) reviewed the geological history of Laysan Island and concluded that it constituted "a refugium for upland and montane lineages able to keep pace, via great adaptive flexibility, with drastic habitat changes." They therefore regarded the biota as an ancient one rather than consisting of recent arrivals. At least as far as birds are concerned, it is unnecessary to postulate such a biotic history, which now appears to be extremely unlikely. The rail

and the millerbird almost certainly colonized Laysan directly from Asia, and their ancestors were anything but montane, being lowland marsh dwellers. The Laysan Duck is but one isolated population of a species now known to have been widespread in various habitats in the main Hawaiian Islands.

Schlanger and Gillett (1976:213) considered that "The Laysan populations of *Himatione* and *Psittirostra* [= *Telespiza*] represent the only known occurrence of the endemic Hawaiian family Drepanidae [sic] on habitats proximal to the beach. Their presence on Laysan lends very strong credence to the concept of a relict, upland biota." The notion that drepanidines are an "upland" group proceeds entirely from the fact that they had been wiped out prehistorically in lowland areas of the main Hawaiian Islands by human-caused habitat destruction. Fossils of ca. 30 species of drepanidines are now known from deposits just above sea level on Kaua'i, O'ahu, and Moloka'i (Olson and James 1982, James and Olson 1991). The Laysan Finch occurs among fossils from O'ahu and Moloka'i, and the Nihoa Finch has been found among fossils from Moloka'i. Fossils of additional forms of *Telespiza* have been found on Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i (James and Olson 1991: 30, and unpubl. data). All were probably most abundant in, or restricted to, more arid, lowland habitats. Fossils of *Himatione* have been found in dune deposits on Kaua'i that were probably never out of the reach of salt spray.

The Hawaiian, as opposed to Asian, component in the avifauna of the Northwestern chain actually consists of formerly widespread, vagile species that, with the possible exception of *Himatione freethii*, have not differentiated in the Northwestern islands. They are neither remnants of an upland biota nor necessarily of ancient occupation.

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